Estuarine, Coastal and Shelf Science 205 (2018) 152–160

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Long-term decline of the canopy-forming algae *Gelidium corneum*, associated to extreme wave events and reduced sunlight hours, in the southeastern Bay of Biscay

Angel Borja*, Guillem Chust, Almudena Fontán, Joxe Mikel Garmendia, María C. Uyarra

AZTI, Marine Research Division, Herrera Kaia, Portualdea s/n, 20100 Pasaia, Spain

ARTICLE INFO

Article history:
Received 4 December 2017
Received in revised form
16 March 2018
Accepted 18 March 2018
Available online 19 March 2018

Keywords:
Climate change
Macroalgae decline
Wave energy
Sunlight
Nutrients
Environmental factors

ABSTRACT

Canopy-forming macroalgae are experiencing large biogeographical shifts due to climate change. One of them (*Gelidium corneum*) has shown a dramatic decline in biomass in northern Spain, in the past 20 years. We investigate here two most plausible hypotheses to explain its decline: (i) a combination of increasing wave energy and decrease of irradiance in the growth season; and (ii) a combination of increasing light in summer and decreasing nutrient concentration. Using a dataset of biomass and environmental variables (1993–2016), in three sectors and three water depths, we have determined that the variables explaining more biomass variability were: suspended solids, nitrate, sunlight hours, significant wave height threshold exceedances (Hs5m), temperature, silicate, and nitrite. When undertaking multiple regression analyses for the whole depth range, only the model including sunlight hours with Hs5m was selected, being highly significant ($p < 0.0001$) and explaining 37% of the variability. When comparing the macroalgal biomass between the initial period of the series (where the biomass was stable) and final period (showing biomass decline), 45% decrease was observed while the Hs5m increase was 41%, detaching the algae from the substratum during the growth season. The decline rate in biomass with time, at each sector and depth, was highly correlated ($p < 0.001$) to the wave energy flux received at each depth, which was higher at 5 m in all sectors, decreasing with depth. In turn, nutrients, instead of decreasing, have increased, and only nitrate presented a significant negative correlation with *G. corneum* biomass, which was not significant after detrending. The significant ($p = 0.001$) increase in rainfall over the studied period can explain the increase of those nutrients. Hence, we question whether the effect of nutrients is such, as already described. The most likely factor explaining the decline of this macroalga was the combination of sunlight hours decrease and Hs5m increase.

© 2018 Elsevier Ltd. All rights reserved.

1. Introduction

Canopy-forming macroalgae are important marine ecosystem components in intertidal and subtidal environments, building relatively large and productive biogenic habitats (Airoldi and Beck, 2007). In recent decades, they have experienced large biogeographical shifts and habitat loss in different areas, such as the North Atlantic (Franco et al., 2018; Southward et al., 1995; Tuya et al., 2012), Australia (Johnson et al., 2011), the Mediterranean (Airoldi et al., 2014), the Baltic Sea (Takolander et al., 2017), and many other regions worldwide (Steneck et al., 2002; Straub et al., 2016). In these areas, canopy-forming macroalgae are being replaced by turf-forming, ephemeral and opportunistic algae, with important structural and functional changes in the associated benthic community (Airoldi et al., 2014; Benedetti-Cecchi et al., 2001; Bianchi et al., 2014; Hawkins et al., 2009; Méndez-Sandín and Fernández, 2016).

These shifts have been attributed to climate change (Harley et al., 2012; Poloczanska et al., 2013), human pressures (Benedetti-Cecchi et al., 2001; Stagnol et al., 2015), or to a combination of both (Airoldi and Beck, 2007; Borja et al., 2013; Crowe et al., 2013; Micheli et al., 2016). The primary drivers of change studied, either in the field or in the laboratory, are temperature, light, acidification (Asnaghi et al., 2013; Porzio et al., 2011; Short et al., 2014), or an interaction of them (Bennett et al., 2015; Bertocci et al., 2014; Diaz-Pulido et al., 2012). In fact, when

* Corresponding author.
E-mail address: aborja@azti.es (A. Borja).

https://doi.org/10.1016/j.ecss.2018.03.016
0272-7714/© 2018 Elsevier Ltd. All rights reserved.

modelling future distribution change scenarios for macroalgae, the main predictor used is temperature change (Franco et al., 2018; Jueterbock et al., 2013; Martínez et al., 2015b). However, other environmental factors, directly or indirectly related to climate change, such as wind and storm regimes, wave energy, or changes in biogeochemical cycles (Franco et al., 2018; Hewitt et al., 2016; Vilibic and Sepic, 2010; Weisse et al., 2014), can play an important role in maintaining or losing canopy-forming macroalgae.

Changes in canopy-forming macroalgae have also been reported for the northern Spain in the past two or three decades (Martínez et al., 2015a), affecting brown species, such as Laminariaceae (Voerman et al., 2013), *Himanthalia elongata* and *Fucus serratus* (Duarte et al., 2013), *Bifurcaria bifurcata* and *Cystoseira baccata* (Méndez-Sandín and Fernández, 2016), red macroalgae, such as *Gelidium corneum* (Borja et al., 2013), or the whole macroalgal community assemblage (Díez et al., 2012; Fernández, 2016; Piñeiro-Corbeira et al., 2016). All authors coincide in suggesting that the main driver for these changes is climate change, and especially the rising temperatures over this temperate zone, which is reducing the cover and abundance of cold-temperate canopy species (e.g., Laminariaceae, fucoids, *H. elongata* and *Chondrus crispus*) and is causing their replacement with warm-temperate species (e.g., *C. baccata, B. bifurcata* and Corallinaceae) (Fernández, 2016). However, in the case of *G. corneum,* which has experienced a dramatic reduction both in cover and biomass in the past 20 years (with an estimated standing stock of >10,000 t in the 1990s and <2000 t since 2015), in the Basque Country (north of Spain), there are two main hypotheses to explain its decline: (i) a combination of increasing wave energy and decrease of irradiance during the growing season (i.e., winter-spring), producing an increase of algae detaching and a decrease of biomass (Borja et al., 2013); and (ii) a combination of increasing light in summer and decreasing nutrient concentration, resulting in bleaching and increasing mortality (Díez et al., 2012; Quintano et al., 2017).

Investigating the most plausible hypothesis of macroalgae shift causes, long-term monitoring data are needed. In some of the abovementioned studies on macroalgae shifts, in the northern Spain, the authors compare two or three short periods within 20–30 years (e.g. (Díez et al., 2012; Duarte et al., 2013; Fernández, 2016; Méndez-Sandín and Fernández, 2016; Piñeiro-Corbeira et al., 2016; Voerman et al., 2013) or are based upon short-term field experiments (Quintano et al., 2017). However, it is well-known that long-term based studies can reveal markedly different results than short-term studies, when addressing climate change (McCoy and Kamenos, 2015). Therefore, the availability of long-term (1993–2016) annual data for *G. corneum* biomass in a large area (>30 km), at three different water depths (5, 10 and 15 m), together with abiotic variables (i.e., temperature, light, significant wave height (Hs5m), nutrients, suspended solids) for the same period, allow to better understand their possible contribution to the decline of *G. corneum* biomass within this ecoregion.

2. Materials and methods

2.1. Study area

The Basque coast is located within the middle latitudes of the eastern North Atlantic Ocean, in the southeastern part of the Bay of Biscay, with a narrow (<20 km) continental platform, and a temperate climate, influenced by the Gulf Stream (Usabiaga et al., 2004). The study area spans ~30 km, between Orio and Higer Cape (Fig. 1), where >60% of the total *G. corneum* biomass of the region is concentrated, being distributed between 0 and 20 m water depth (Borja, 1987, 1988). For management reasons, the area was divided into three sectors of around 10 km each, for biomass calculation (Borja, 1987) (Fig. 1).

Due to the location and orientation of the Basque coast, in relation to the North Atlantic low-pressure systems, the study area is exposed to large storms from the NW, resulting in strong swell waves (Galparsoro et al., 2010; González et al., 2004; Liria et al., 2009).

2.2. Environmental variables

Light, temperature, nutrients and wave exposure have been described as factors affecting *Gelidium* spp. productivity (Duarte, 1995; Duarte and Ferreira, 1993; Prathep et al., 2009; Torres et al., 1991). Optimum Sea Surface Temperatures (SST) for *G. corneum* growth have been defined at between 10 °C and 25 °C, with higher temperatures being a possible cause for bleaching (Santelices, 1991). Light and nutrients have a positive influence on the biomass production, whilst storms have a negative influence, detaching algae from the substratum. Other variables, such as suspended solids and turbidity can have a negative effect, reducing the light received by *G. corneum* in case of increase. Therefore, the minimum biomass of *G. corneum* is found in winter, with the maximum in summer (Borja, 1994).

To study the effect of environmental variables on *G. corneum* biomass, we obtained physico-chemical variables data from the Basque Water Agency, which has monitored the Basque coast quarterly in 16 stations, between 1995 and 2016 (Borja et al., 2016). From these stations, the data from the five stations located in the proximity to the *G. corneum* sampled sectors (Fig. 1) have been used here. Sampling and analysing methods within this monitoring network have been described elsewhere (e.g. Borja et al., 2016), and detailed information for physico-chemistry analysis can be found in Bald et al. (2005) and Tueros et al. (2009). The variables analysed were SST, oxygen saturation, ammonium, nitrate, nitrite, orthophosphate, silicate, suspended solids, and turbidity. Since *G corneum* is sampled in June, mean values for these variables were calculated for January–June each year. In the case of SST, also mean values for July–June were calculated. It should be noted that no data exist for these physico-chemical variables, excepting SST, for 1993 and 1994.

In addition, Borja et al. (2004) determined for the Basque coast that the sunlight hours (as a proxy of the irradiance received), in the preceding winter and spring seasons, correlated significantly ($p < 0.05$) with the June standing stock of *G. corneum*. Hence, daily sunlight hours, recorded at the Donostia-San Sebastián Meteorological Observatory between 1993 and 2016, together with the daily SST recorded at the Donostia-San Sebastián Aquarium (for details of this series, see Goikoetxea et al. (2009)), were collated. Subsequently, the total number of sunlight hours and the mean SST for the period January–June were determined for each year. As the second hypothesis includes the effect of sunlight in summer, we calculated the number of sunlight hours received in the previous summer (July–September) to be compared with the biomass available next June.

Finally, *G. corneum* is detached from the substratum in autumn and winter, due to partial losses of branches (Gorostiaga, 1994), following NW storms (Borja, 1987). Borja (1994) studied wave conditions favouring the macroalgae detachment, and established a threshold on the significant wave height (Hs) of 5 m, necessary to produce the breaking of the algae. In this study, hourly wave Hs data, for the period 1993–2016, from the SIMAR database (supplied by "Puertos del Estado", www.puertos.es/en-us/oceanografia/Pages/portus.aspx) at the grid point 1068075 (43.65ºN, 3.00ºW) were used. The Hs at this point shows a good agreement with the nearest offshore buoy (the Bilbao-Vizcaya buoy), with a correlation coefficient of 0.94, a root mean square difference of 0.45 m, and a

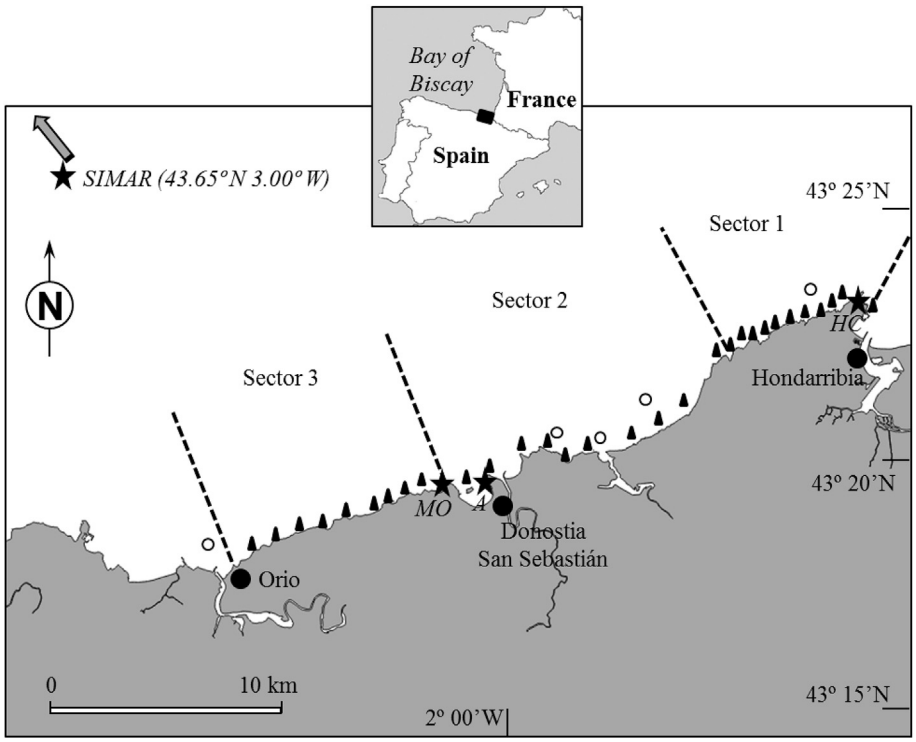

Fig. 1. Study area, within the eastern part of the Basque coast (Bay of Biscay). Transect sampled (black triangles), together with the sectors determined for *Gelidium corneum* biomass calculation; MO = Donostia-San Sebastián Meteorological Observatory; HC=Higer Cape, A = Donostia-San Sebastián Aquarium; SIMAR=SIMAR grid point 1068075; and the Water Quality Monitoring Network stations for physico-chemical samples (o) are presented.

bias (model minus observations) of −0.16 m. The Hs data at the SIMAR grid point has nearly full temporal coverage, with only 1% of missing data (whilst the buoy has many data gaps, especially during severe storms). Here, the number of times exceeding the threshold of 5 m in Hs (hereinafter referred to as Hs5m), for the period January–June, has been defined as a proxy of wave exposure affecting *G. corneum* growth.

2.3. Sampling and standing stock biomass determination

The area was sampled for *G. corneum* in 1983 and 1986 (Borja, 1987), but after 1993 the surveys were undertaken on an annual basis, always between 10th and 20th June (Borja et al., 2013). During the whole period, the surveys were carried out in a similar manner, with the participation of the same team of divers, ensuring consistency and comparability throughout the time series, following the methodology of Borja (1987). Within each sector, several transects, separated by approximately 1 km, were sampled (11 transects in Sector 1; 10 in Sector 2; and 9 in Sector 3 (Fig. 1)). Within each transect, *G. corneum* samples were collected at 5, 10 and 15 m water depths (after correcting for the tide and position fixing, by GPS), by SCUBA diving, using sampling squares of 50 × 50 cm (Alvarez De Meneses, 1972), in areas where *G. corneum* was consistently dominant. All algae fitting within the square was picked out by hand and placed into a mesh bag to be brought to the boat.

In addition, the *G. corneum* cover, within a radius of 5 m at the same depth of each sampling location, was recorded following a semiquantitative scale, based upon the Braun-Blanquet (1932) scale: (0) absence; (1) isolated individuals, very rare presence (1–4%); (2) very small groups of individuals (5–24%); (3) disperse presence of *G. corneum* (25–49%); (4) large *G. corneum* patches (50–74%); (5) small parts uncover by *G. corneum* (75–99%); and (6) continuous cover (100%).

In the laboratory, epiphytes were removed, and fresh biomass was determined by weighting samples after 5 min of centrifugation at 1000 r.p.m., for water removal. Subsequently, the biomass was extrapolated to 1 m^2.

The standing stock biomass was calculated following the method described by Mann (1972) and Niell and Soneira (1976). The total biomass of a sector was estimated as the mean sector biomass over 1 m^2, multiplied by the band width and the length of the sector with the presence of *G. corneum*.

2.4. Statistical analysis

We first analysed statistically the trend of *G. corneum* biomass throughout time, to confirm and quantify the rate of biomass decline, using a Linear Model (Chambers, 1992; Wood, 2006), where the Biomass (B) is modelled as a function of two categorical variables so-called factors (depth and sector, with 3 levels each), time (Year) and the interactions among them (*Depth:Year, Sector:Year, Depth:Sector*): *B (Year, Depth, Sector) ~ f(Depth + Sector + Depth:Year + Sector:Year + Depth:Sector)*. Based on the sign (positive or negative) of the interaction coefficients terms with year and its statistical significance (via the analysis of variance -ANOVA-of the model), we tested whether biomass decline is general or site/depth dependent. We were also particularly interested to statistically test whether the depth influences the rate of biomass decrease. In this way, we used all *G. corneum* biomass data (216 observations, and not only the annual average values, n = 22–24).

Secondly, we undertook a further analysis to test whether environmental variables could explain the variability and decline of *G. corneum* biomass, following our two hypotheses (i.e. influence of sunlight and waves during the growth season, and influence of

sunlight during previous summer and nutrients during the growth season), as well as other potential drivers (i.e. increase of temperature, changes in turbidity, etc.). As environmental variables were not available at different depths, we averaged the three sectors and three sampling depths at each transect, using all sampling stations. In order to avoid spurious correlation between temporally-autocorrelated series (Legendre and Legendre, 2012), we analysed first the trend of time series for each variable using a linear regression model. In the case that both response and environmental variables (sunlight hours, Hs5m and water properties) had a significant trend with time, we detrended both variables prior to the linear regression analysis, by subtracting the estimated trend value to the raw value. We used a linear regression analysis between *G. corneum* biomass and environmental variables (sunlight hours, Hs5m and water properties), each variable separately and all together with variable selection method. The model selection was carried out applying the second-order Akaike Information Criterion (AICc); recommended for small sample sizes (Burnham and Anderson, 2002). In particular, for model selection we start from a subset of variables (i.e. the significant ones, excluding those not significant after detrending) and then used *dredge* function of 'MuMIn' R language to compare all possible combinations of terms and select the best one based on lowest AICc (Barton, 2016). This means that we had 24 (1993–2016) or 22 (1995–2016) pairs of data, depending on the availability of the abiotic variables.

3. Results

3.1. Time series analysis of G. corneum by depth and sector

The trend analysis between *G. corneum* biomass and factors (depths and sectors), throughout time (1993–2016), showed that all terms, including the interaction terms, were significant ($p < 0.0001$) (Table 1). The linear model *Depth* + *Sector* + *Depth:Year* + *Sector:Year* + *Depth:Sector* explained 86% of the variance with all terms significant ($p < 0.0001$). The coefficients of the interaction terms with time are negative (Table 2 and Fig. 2), indicating that the decline of *G. corneum* biomass is general since occurs in all depths and sectors.

By plotting the linear model (Fig. 2), it is also possible to observe that the decrease of *G. corneum* biomass throughout the studied period was higher at lower depth (5 m) than at 10 m, and, specially, than at 15 m. The decay in biomass was stronger in Sector 1 than in Sectors 3 and 2, at any depth (Fig. 2).

3.2. Analysis of environmental drivers

For the single variable analyses, significant ($p < 0.05$) correlation was found between *G. corneum* biomass, in the whole depth range (5–15 m), and, in decreasing order of explained variability, suspended solids, nitrate, sunlight hours (January–June), Hs5m, sunlight hours (previous summer), average SST from July to June and from January to June, silicate, and nitrite (Table 3). All of them were negatively related to biomass, except sunlight in January–June, which was related positively. However, among all these correlated variables, SST (July–June), sunlight hours (previous summer), nitrate, nitrite, silicate and suspended solids presented significant linear trends with time ($p < 0.05$); hence, we detrended their time series. After detrending for time, the residuals of these variables were not correlated significantly with *G. corneum* biomass (Table 3). The Hs5m was more correlated with *G. corneum* at 5 m biomass than with overall biomass (5–15 m depth) (Table 3).

When undertaking multiple regression analyses for the whole depth range, using only the variables for which the correlation was significant alone, only the model including sunlight hours from January to June with Hs5m was selected, being highly significant ($p < 0.0001$) and explaining 37% of the variability (Table 3). The same model was selected at 5 m, increasing the explained variability until 41% (Table 3).

The regression models between the main individual variables correlating significantly ($p < 0.05$) with *G. corneum* biomass, as determined in Table 3, are represented in Fig. 3. The number of sunlight hours had a positive correlation with *G. corneum* biomass, whilst the Hs5m had a negative correlation.

Regarding the multiple regression model, the predictions of the model selected in Table 3 have been plotted against the observed *G. corneum* biomass in Fig. 4, showing the good accuracy in the case of total biomass and at 5 m depth.

Table 1
Linear model between *Gelidium corneum* biomass and factors (depth, sector, year).

Factor	Pr(>|t|)
Depth	<0.0001
Sector	<0.0001
Depth:Sector	<0.0001
Depth:Year	<0.0001
Sector:Year	<0.0001

Adjusted R-squared: 0.8584.
p-value: < 0.0001.

Table 2
Slope of the linear model where *Gelidium corneum* biomass change throughout years as a function of depth and sector factors.

	Depth 5 m	Depth 10 m	Depth 15 m
Sector 1	−111.3	−71.8	−41.2
Sector 2	−71.6	−32.0	−1.5
Sector 3	−76.1	−36.6	−6.1

4. Discussion

One of the variables explaining more variability in *G. corneum* decline was Hs5m, especially at shallower depth (5 m, see Table 3). The biomass of *G. corneum* was stable during 1993–2005 whereas a decline in biomass was observed for the 2006–2016. Within these periods, differences in the Hs5m were also evident: (i) 1993–2005, in which 6 out of 13 years the Hs exceeded >100 times 5 m; and (ii) 2006–2016, in which the exceedance was in 8 out of 11 years. When comparing both periods, the increase in the Hs5m was 41% (Table 4), which could affect the algae, detaching it from the substratum during the growth season (comparing both periods the decrease of macroalgae biomass was 45%, Table 4).

This detaching effect seems to be higher in Sector 1 than in Sectors 2 and 3, being much higher at 5 m, than at 10 and, especially, 15 m. The stress and disturbance caused by wave exposure on this and other macroalgae species have been described elsewhere (Borja et al., 2013; England et al., 2008; Nishihara and Terada, 2010; Prathep et al., 2009; Wernberg and Connell, 2008). In fact, the decline rate in biomass with time, at each sector and depth (as shown in Fig. 2), was highly correlated ($p < 0.001$) to the wave energy flux received at each depth, which was higher at 5 m in all sectors, and decreased with depth, but also the wave energy flux was higher in Sector 1 than in Sectors 2 and 3 (Fig. 5). This mean bottom wave energy flux has been calculated after extracting the energy flux values at each sampling location, from Galparsoro et al. (2012).

Our findings indicate that the biomass decline occurred at all studied depths, with an important gradient that gets reduced from

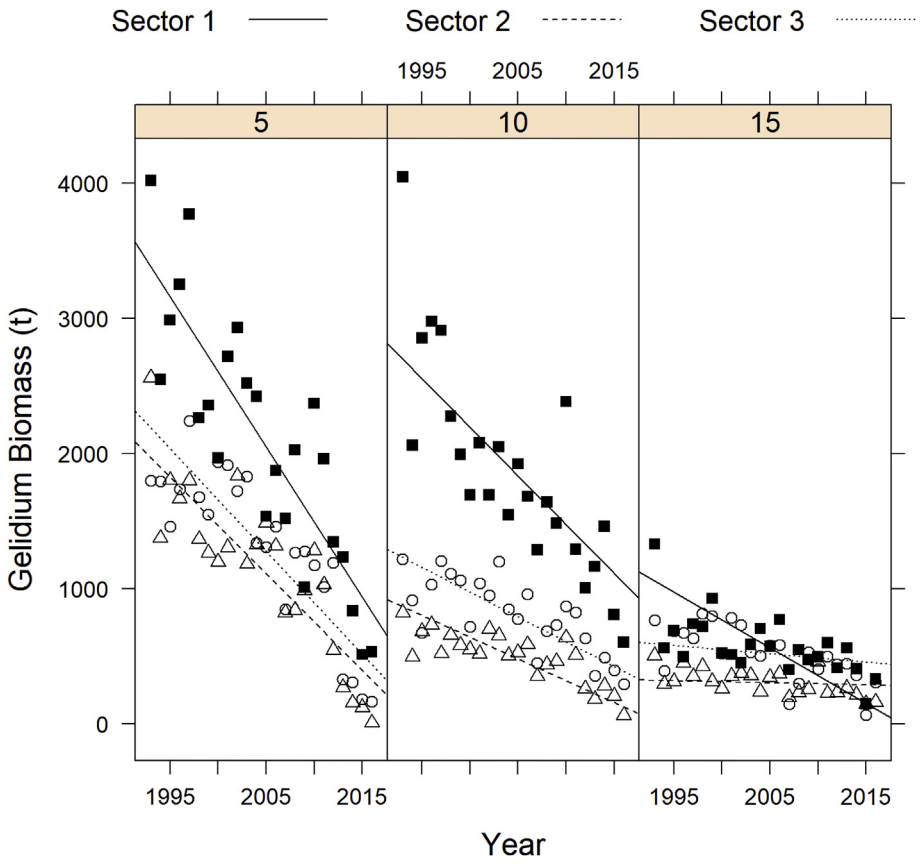

Fig. 2. Linear model results of the effects of time (year), depth (5, 10, 15 m) and Sector on *Gelidium corneum* biomass. Sector 1: squares, Sector 2: triangles, Sector 3: circles.

Table 3
Temporal trends and regression between individual environmental variables and *Gelidium corneum* biomass, as well as multiple regression with two variables, at the whole depth range (5–15 m) and only at 5 m depth. Note that the periods differ, depending on the availability of data, and calculations were undertaken for mean values of the variables between January and June, except for Sea Surface Temperature (SST) and sunlight hours. In some cases, the calculation was undertaken after detrending the series. Hs5m: significant wave height threshold exceedance (above 5 m). Significant p-values (<0.05) are highlighted in bold.

Period	Variables	Temporal trend		Model for *G. corneum* biomass (5–15 m depth)			
		p-value	R	p-value	R	Adjusted r^2	Regression Coefficient
1993–2016	SST (July–June)	**0.0440**	0.414	**0.0244**	−0.458	0.209	−2139.1
1993–2016	SST (July–June) (detrended)	-	–	0.2656	0.236	0.013	0.141
1993–2016	SST (January–June)	0.3640	0.194	0.3231	−0.211	0.044	−1019.0
1993–2016	Sunlight hours (January–June)	0.2870	−0.212	**0.0044**	0.561	0.283	17.78
1993–2016	Sunlight hours (July–September)	**0.0007**	0.642	**0.0065**	−0.538	0.258	−25.35
1993–2016	Sunlight hours (July–Sep) (detrended)	–	–	0.6313	−0.103	−0.034	2.83
1993–2016	Hs5m	0.2613	0.238	**0.0315**	−0.439	0.156	−12.01
1995–2016	Oxygen Saturation	0.3989	0.189	0.2004	−0.283	0.034	−166.0
1995–2016	Ammonium	0.4977	0.153	0.2527	−0.254	0.018	−19481.7
1995–2016	Nitrate	<**0.0001**	0.765	**0.0006**	−0.672	0.424	−15521.0
1995–2016	Nitrate (detrended)	-	-	0.6646	0.098	−0.039	1445.0
1995–2016	Nitrite	**0.0366**	0.447	0.0550	−0.414	0.130	−206017.0
1995–2016	Orthophosphate	0.6973	−0.087	0.8293	0.048	−0.047	11671.0
1995–2016	Silicate	**0.0243**	0.478	**0.0287**	−0.466	0.178	−559.5
1995–2016	Silicate (detrended)	-	-	0.7104	−0.083	−0.042	−47.13
1995–2016	Suspended Solids	<**0.0001**	0.784	<**0.0001**	−0.760	0.556	−537.0
1995–2016	Suspended Solids (detrended)	-	-	0.4276	−0.178	−0.016	−100.1
1995–2016	Turbidity	0.2699	−0.245	0.1861	0.292	0.039	1947.0
1993–2016	Sunlight hours + Hs5m	-	-	**0.0028**	-	0.373	15.65, −9.38, respectively
		Temporal trend		Model for *G. corneum* biomass at 5 m depth			
Period	Variables	p-value	R	p-value	R	Adjusted r^2	Regression Coefficient
1993–2016	Hs5m	0.2613	0.238	**0.0161**	−0.485	0.200	−11.10
1993–2016	Sunlight hours + Hs5m	-	-	**0.0014**	-	0.410	12.85, −8.93, respectively

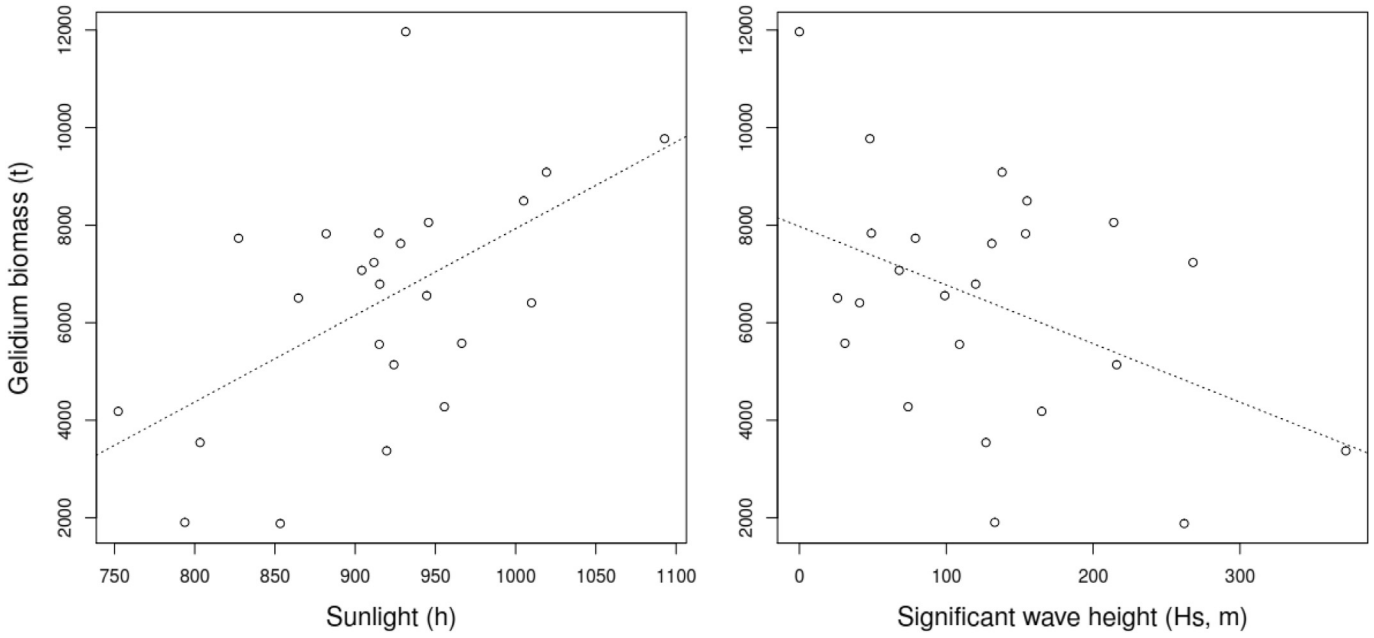

Fig. 3. Regression between main variables correlating significantly ($p < 0.05$) with *Gelidium corneum* biomass, as determined in Table 3.

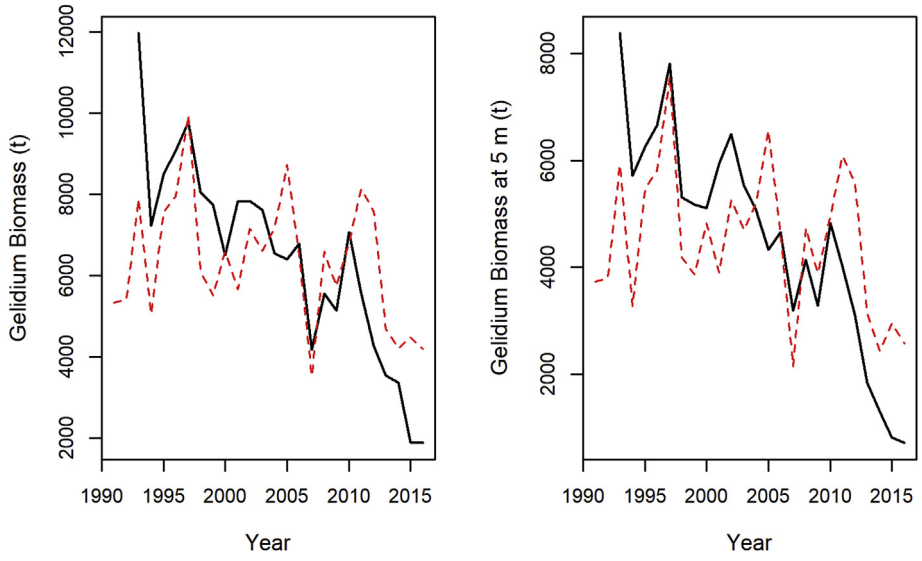

Fig. 4. *Gelidium corneum* biomass observations (Black line) summed for the three depths (left) and at 5 m depth (right), compared with the corresponding model predictions: Sunlight hours + Significant wave height threshold exceedance (red dashed). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 4
Comparison of the mean values for different variables, for two periods, showing the percentage of increase or decrease, related to the initial period. Hs: significant wave height threshold exceedance; SS: Suspended Solids.

Variable	Units	1993–2005	2006–2016	Increase/Decrease (%)
Biomass	(t)	8084	4482	−44.6
Sunlight (January–June)	(h)	944	882	−6.6
Sunlight (July–September)	(h)	563	618	9.8
Hs	(nr)	108	152	40.74
Ammonium	($\mu m\ l^{-1}$)	0.043	0.058	34.65
Nitrate	($\mu m\ l^{-1}$)	0.185	0.297	60.54
Nitrite	($\mu m\ l^{-1}$)	0.011	0.014	27.27
Phosphate	($\mu m\ l^{-1}$)	0.028	0.028	1.95
Silicate	($\mu m\ l^{-1}$)	3.505	4.710	34.38
SS	($mg\ l^{-1}$)	2.092	6.235	198.04
Turbidity	(NTU)	0.802	0.614	−23.4

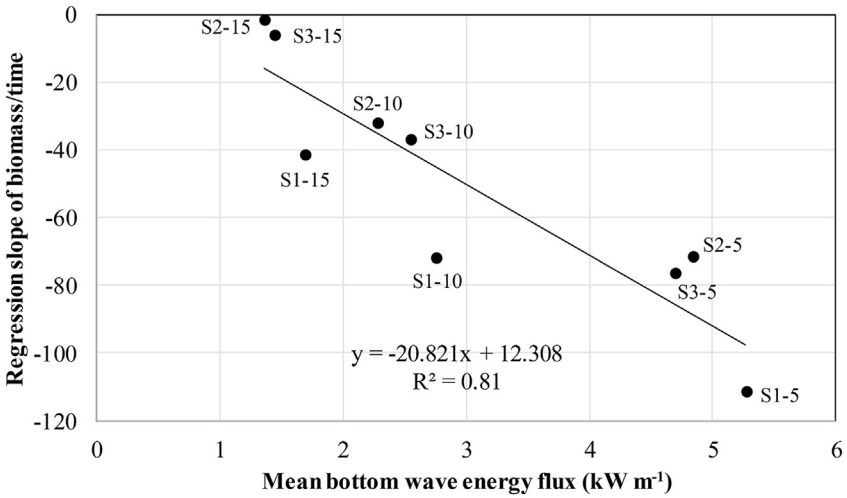

Fig. 5. Regression between the mean bottom wave energy flux and the regression slopes between *Gelidium corneum* biomass observations with time, at three depths (5, 10, 15 m) and three sectors (S1, S2, S3).

5 to 15 m (see Fig. 2). When studying other individual factors determining the *G. corneum* biomass, its correlation with sunlight hours during the growth season was firstly described by Borja et al. (2004), existing abundant bibliography on the importance of irradiance for this species (Carmona et al., 1996; Mercado et al., 2001; Silva et al., 1998). However, the relationship found here indicates that, in the long-term series, sunlight hours have decreased in the area, in winter-spring (near 7%, when comparing the two periods, Table 4), possibly explaining partially the biomass decline. In turn, other authors found (Quintano et al., 2017), based on summer experiments, that an increase of summer irradiance could result in apical bleaching and further mortality of *G. corneum* in shallow waters. In fact, we have detected here a positive trend in summer sunlight, which was not significant after detrending, representing an increase of near 10% in the two periods of Table 4. Therefore, it seems that, although increasing irradiance in summer can cause bleaching and some mortality of the species, this increase was not enough to explain the biomass decline, since the statistical effect was not significant.

Suspended solids concentration, which was the single variable explaining more variability (56%) in *G. corneum* biomass (but it was not significant after detrending), was probably caused by strong waves since both variables were correlated, and the Hs5m was also negatively correlated with biomass. In fact, when comparing the periods mentioned in Table 4, the mean suspended solids concentration in the second period was 6.2 mg l^{-1}, whilst in previous years the concentration was always 2.1 mg l^{-1}; thus, the concentration for the period 2006–2016 was 198% higher than in the period 1993–2005. This increasing concentration of suspended solids can result in a decrease of light received, especially at deeper samples (Silva et al., 1998), and finally in less biomass. However, there are three factors which let us think that the increasing concentration of solids is merely a proxy of the wave energy: (i) the maximum biomass decrease was at shallower depths, not at deeper, in which the reduction of irradiance should be maximum; (ii) the concentration of solids in the most recent period was much below the 15 mg l^{-1} recommended as one of the habitat requirements for growth and survival of submerged vegetation in Chesapeake Bay (Batiuk et al., 2000), and (iii) after detrending the concentration of suspended solids, the correlation with *G. corneum* was not significant, indicating that the correlation found could be due to the temporal autocorrelation of the two time series.

Regarding nutrients, Díez et al. (2012) hypothesized a decrease in summer rainfall in the Basque coast, since 1980, which, associated with the increasing water treatment in the region, has resulted in nutrient depletion. According to these authors, this fact, together with increasing temperature and water transparency in summer, may act synergistically to reduce *G. corneum* biomass. However, after our results, instead of decreasing, nutrients presented an increase since 1995 (nitrate 61%, nitrite 27%, phosphate 1.9%, ammonium 35%, and silicate 34%, Table 4), and only nitrate presented a significant negative correlation with *G. corneum* biomass, which was not significant after detrending. In all cases, nutrient concentrations were not excessively high (mean ± standard deviation values, for 1995–2016: ammonium 0.05 ± 0.03 μm l^{-1}, nitrate 0.24 ± 0.09 μm l^{-1}, nitrite 0.01 ± 0.004 μm l^{-1}, phosphate 0.03 ± 0.009 μm l^{-1}, silicate 4.1 ± 1.8 μm l^{-1}). In fact, in a large investigation in the Basque Country, on the effects of water treatment in the whole region, Borja et al. (2016) found that most physico-chemical and biological variables improved after sanitation, but very few worsened (i.e. suspended solids, nitrate and silicate). Those authors determined a significant ($p = 0.0001$) increase in rainfall over the studied period (1995–2014), which can explain the increase of nitrate and silicate.

Hence, taking into account that, during the period 1993–2016, the sunlight hours for the *G. corneum* growth season (January–June) have decreased and the nutrient concentrations have increased, both facts question the acceptability of the hypothesis proposed by Díez et al. (2012) and Quintano et al. (2017). These authors tried to explain the lower *Gelidium* biomass by a combination of increasing light and decreasing nutrient concentration, resulting in bleaching and increasing mortality, which has not been proven with our data and analysis.

In turn, the first hypothesis (a combination of wave energy and irradiance, resulting in a decrease of biomass (Borja et al., 2013)), can be accepted, since the two significant models selected when combining several variables, were those including sunlight hours and Hs5m.

G. corneum, which in the Basque coast achieves its northern limit with a continuous population, probably is at the boundary of its physiological requirements (Luning, 1990). Hence, when the system was more or less stable (i.e. from 1993 to 2005), the main single factor explaining the existing biomass was the sunlight hours during the growth season, as determined by Borja et al. (2004).

However, when the wave regime changed after 2006, with most years having a high number of Hs5m exceedances over the threshold necessary to detach the algae, the combination of both variables has become the explaining factor of the existing biomass. As the high number of large waves has been repeated many years since then, their accumulated effect may be the cause for the dramatic depletion of biomass and, probably, in a range shift of the communities as detected in other species in Europe (Mineur et al., 2015). In some cases, these changes can lead to a regime shift in which the system is not able to return to the previous state, even after decades (Duarte et al., 2009).

These findings can be important when modelling future distributional population scenarios for *G. corneum* under climate change, since, although the increasing temperature can result in population shifts, it cannot be used as the main predictor for habitat suitability at local or regional scales. In turn, sunlight hours, wave energy, or suspended solid changes should also be considered in future distributional population scenarios.

Acknowledgements

AZTI's sampling and laboratory technicians' teams have provided support in collecting and analysing samples during this extended period of time. “Puertos del Estado” has supplied significant wave height data from the SIMAR database. The Spanish Meteorological Agency and the Aquarium, San Sebastián, provided us kindly with daily sunlight hours and sea surface temperature, respectively. Manuel González and Pedro Liria (AZTI) undertook some of the wave calculations. The Basque Water Agency has provided environmental data. The Directorate of Fishing and Aquaculture, from the Basque Government, funded this project since 1986. This is contribution 860 from the Marine Research Division (AZTI).

References

Airoldi, L., Ballesteros, E., Buonuomo, R., van Belzen, J., Bouma, T.J., Cebrián, E., De Clerck, O., Engelen, A.H., Ferrario, F., Fraschetti, S., Gianni, F., Guidetti, P., Ivesa, L., Mancuso, F.P., Micheli, F., Perkol-Finkel, S., Serrao, E.A., Strain, E.M., Mangialajo, L., 2014. Marine forests at risk: solutions to halt the loss and promote the recovery of Mediterranean canopy-forming seaweeds. In: Proceedings of the 5th Mediterranean Symposium on Marine Vegetation, pp. 28–33. Portoroz, Slovenia.

Airoldi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe. Oceanography and Marine Biology - An Annual Review 45, 345–405.

Alvarez De Meneses, A., 1972. Contribución al conocimiento de los campos de algas del Cantábrico. Boletín del Instituto Español de Oceanografía 154, 1–35.

Asnaghi, V., Chiantore, M., Mangialajo, L., Gazeau, F., Francour, P., Alliouane, S., Gattuso, J.-P., 2013. Cascading effects of ocean acidification in a rocky subtidal community. PLoS One 8, e61978.

Bald, J., Borja, A., Muxika, I., Franco, J., Valencia, V., 2005. Assessing reference conditions and physico-chemical status according to the European water framework directive: a case-study from the Basque Country (northern Spain). Marine Pollution Bulletin 50, 1508–1522.

Barton, K., 2016. MuMIn: Multi-model Inference. R Package Version 1.15.6.

Batiuk, R.A., Bergström, P., Kemp, M., Koch, E., Murray, L., Stevenson, J.C., Bartleson, R., Carter, V., Rybicki, N.B., Landwehr, J.M., Gallegos, C., Karrh, L., Naylor, M., Wilcox, D., Moore, K.A., Ailstock, S., Teichberg, M., 2000. Chesapeake bay submerged aquatic vegetation water quality and habitat-based requirements and restoration targets: a second technical synthesis. United States Environmental Protection Agency for the Chesapeake Bay Program 231.

Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P.S., Airoldi, L., Relini, G., Cinelli, F., 2001. Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. Marine Ecology Progress Series 214, 137–150.

Bennett, S., Wernberg, T., de Bettignies, T., Kendrick, G.A., Anderson, R.J., Bolton, J.J., Rodgers, K.L., Shears, N.T., Leclerc, J.-C., Lévèque, L., Davoult, D., Christie, H.C., 2015. Canopy interactions and physical stress gradients in subtidal communities. Ecology Letters 18, 677–686.

Bertocci, I., Seabra, M.I., Dominguez, R., Jacinto, D., Ramírez, R., Coca, J., Tuya, F., 2014. Effects of loss of algal canopies along temperature and irradiation gradients in continental Portugal and the Canary Islands. Marine Ecology Progress Series 506, 47–60.

Bianchi, C.N., Corsini-Foka, M., Morri, C., Zenetos, A., 2014. Thirty years after: dramatic change in the coastal marine ecosystems of Kos Island (Greece), 1981-2013. Mediterranean Marine Science 15, 482–497.

Borja, A., 1987. Cartografía, evaluación de la biomasa y arribazones del alga *Gelidium sesquipedale* (Clem.) Born. et Thur. en la costa guipuzcoana (N España). Investigación Pesquera 51, 199–224.

Borja, A., 1988. Cartografía y evaluación de la biomasa del alga *Gelidium sesquipedale* (Clem.) Born. et Thur. 1876 en la costa vizcaína (N. de España). Investigación Pesquera 52, 85–107.

Borja, A., 1994. Factores ambientales que influyen en al generación, desprendimiento de biomasa, crecimiento y producción en praderas naturales de *Gelidium sesquipedale* (Clem.) Born. et Thur. en el País Vasco (N de España). Scientia Marina 58, 251–260.

Borja, A., Aguirrezabalaga, F., Martínez, J., Sola, J.C., García-Arberas, L., Gorostiaga, J.M., 2004. Benthic communities, biogeography and resources management. In: Borja, A., Collins, M. (Eds.), Oceanography and Marine Environment of the Basque Country, vol. 70. Elsevier Oceanography Series, pp. 455–492.

Borja, Á., Chust, G., Rodríguez, J.G., Bald, J., Belzunce-Segarra, M.J., Franco, J., Garmendia, J.M., Larreta, J., Menchaca, I., Muxika, I., Solaun, O., Revilla, M., Uriarte, A., Valencia, V., Zorita, I., 2016. The past is the future of the present': learning from long-time series of marine monitoring. Science of The Total Environment 566–567, 698–711.

Borja, Á., Fontán, A., Muxika, I., 2013. Interactions between climatic variables and human pressures upon a macroalgae population: implications for management. Ocean & Coastal Management 76, 85–95.

Braun-Blanquet, J., 1932. Plant Sociology: the Study of Plant Communities (Ed. G.D. Fuller and H.S. Conard). MacGraw-Hill, New York, p. 439.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-model Inference: a Practical Information-theoretic Approach. Springer.

Carmona, R., Vergara, J.J., Pérez-Lloréns, J.L., Figueroa, F.L., Niell, F.X., 1996. Photosynthetic acclimation and biochemical responses of Gelidium sesquipedale cultured in chemostats under different qualities of light. Marine Biology 127, 25–34.

Chambers, J.M., 1992. Linear models. In: Chambers, J.M., Hastie, T.J. (Eds.), Statistical Models in S. Wadsworth & Brooks/Cole.

Crowe, T.P., Cusson, M., Bulleri, F., Davoult, D., Arenas, F., Aspden, R., Benedetti-Cecchi, L., Bevilacqua, S., Davidson, I., Defew, E., Fraschetti, S., Golléty, C., Griffin, J.N., Herkül, K., Kotta, J., Migné, A., Molis, M., Nicol, S.K., Noël, L.M.L.J., Pinto, I.S., Valdivia, N., Vaselli, S., Jenkins, S.R., 2013. Large-scale variation in combined impacts of canopy loss and disturbance on community structure and ecosystem functioning. PLoS One 8 e66238.

Diaz-Pulido, G., Anthony, K.R.N., Kline, D.I., Dove, S., Hoegh-Guldberg, O., 2012. Interactions between ocean acidification and warming on the mortality and dissolution of coralline algae. Journal of Phycology 48, 32–39.

Díez, I., Muguerza, N., Santolaria, A., Ganzedo, U., Gorostiaga, J.M., 2012. Seaweed assemblage changes in the eastern Cantabrian Sea and their potential relationship to climate change. Estuarine, Coastal and Shelf Science 99, 108–120.

Duarte, C., Conley, D., Carstensen, J., Sánchez-Camacho, M., 2009. Return to Neverland: shifting baselines affect Eutrophication restoration targets. Estuaries and Coasts 32, 29–36.

Duarte, L., Viejo, R.M., Martínez, B., deCastro, M., Gómez-Gesteira, M., Gallardo, T., 2013. Recent and historical range shifts of two canopy-forming seaweeds in North Spain and the link with trends in sea surface temperature. Acta Oecologica 51, 1–10.

Duarte, P., 1995. A mechanistic model of the effects of light and temperature on algal primary productivity. Ecological Modelling 82, 151–160.

Duarte, P., Ferreira, J.G., 1993. A methodology for parameter estimation in seaweed productivity modelling. Hydrobiologia 260, 183–189.

England, P.R., Phillips, J., Waring, J.R., Symonds, G., Babcock, R., 2008. Modelling wave-induced disturbance in highly biodiverse marine macroalgal communities: support for the intermediate disturbance hypothesis. Marine and Freshwater Research 59, 515–520.

Fernández, C., 2016. Current status and multidecadal biogeographical changes in rocky intertidal algal assemblages: the northern Spanish coast. Estuarine, Coastal and Shelf Science 171, 35–40.

Franco, J.N., Tuya, F., Bertocci, I., Rodríguez, L., Martínez, B., Sousa-Pinto, I., Arenas, F., 2018. The ‘golden kelp’ *Laminaria ochroleuca* under global change: integrating multiple eco-physiological responses with species distribution models. Journal of Ecology 106, 47–58.

Galparsoro, I., Borja, Á., Legorburu, I., Hernández, C., Chust, G., Liria, P., Uriarte, A., 2010. Morphological characteristics of the Basque continental shelf (bay of Biscay, northern Spain); their implications for integrated coastal zone management. Geomorphology 118, 314–329.

Galparsoro, I., Liria, P., Legorburu, I., Bald, J., Chust, G., Ruiz-Minguela, P., Pérez, G., Marqués, J., Torre-Enciso, Y., González, M., Borja, A., 2012. A Marine Spatial Planning approach to select suitable areas for installing wave energy converters on the Basque continental shelf (Bay of Biscay). Coastal Management 40, 1–9.

Goikoetxea, N., Borja, Á., Fontán, A., González, M., Valencia, V., 2009. Trends and anomalies in sea-surface temperature, observed over the last 60 years, within the southeastern Bay of Biscay. Continental Shelf Research 29, 1060–1069.

González, M., Uriarte, A., Fontán, A., Mader, J., Gyssels, P., 2004. Marine dynamics. In: Borja, A., Collins, M. (Eds.), Oceanography and Marine Environment of the Basque Country, vol. 70. Elsevier Oceanography Series, pp. 133–157.

Gorostiaga, J.M., 1994. Growth and production of the red alga *Gelidium sesquipedale* off the Basque coast (northern Spain). Marine Biology 120, 311–322.

Harley, C.D.G., Anderson, K.M., Demes, K.W., Jorve, J.P., Kordas, R.L., Coyle, T.A., Graham, M.H., 2012. Effects of climate change on global seaweed communities. Journal of Phycology 48, 1064–1078.
Hawkins, S.J., Sugden, H.E., Mieszkowska, N., Moore, P.J., Poloczanska, E., Leaper, R., Herbert, R.J.H., Genner, M.J., Moschella, P.S., Thompson, R.C., Jenkins, S.R., Southward, A.J., Burrows, M.T., 2009. Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. Marine Ecology Progress Series 396, 245–259.
Hewitt, J.E., Ellis, J.I., Thrush, S.F., 2016. Multiple stressors, nonlinear effects and the implications of climate change impacts on marine coastal ecosystems. Global Change Biology 22, 2665–2675.
Johnson, C.R., Banks, S.C., Barrett, N.S., Cazassus, F., Dunstan, P.K., Edgar, G.J., Frusher, S.D., Gardner, C., Haddon, M., Helidoniotis, F., Hill, K.L., Holbrook, N.J., Hosie, G.W., Last, P.R., Ling, S.D., Melbourne-Thomas, J., Miller, K., Pecl, G.T., Richardson, A.J., Ridgway, K.R., Rintoul, S.R., Ritz, D.A., Ross, D.J., Sanderson, J.C., Shepherd, S.A., Slotwinski, A., Swadling, K.M., Taw, N., 2011. Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. Journal of Experimental Marine Biology and Ecology 400, 17–32.
Jueterbock, A., Tyberghein, L., Verbruggen, H., Coyer, J.A., Olsen, J.L., Hoarau, G., 2013. Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal. Ecology and Evolution 3, 1356–1373.
Legendre, P., Legendre, L., 2012. Numerical Ecology, vol. 24. Elsevier, Amsterdam, p. 1006.
Liria, P., Garel, E., Uriarte, A., 2009. The effects of dredging operations on the hydrodynamics of an ebb tidal delta: Oka Estuary, northern Spain. Continental Shelf Research 29, 1983–1994.
Luning, K., 1990. Seaweeds. Their Environment, Biogeography and Ecophysiology. John Wiley & Sons, New York, pp. 1–527.
Mann, K.H., 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. I. Zonation and biomass of seaweeds. Marine Biology 12, 1–10.
Martínez, B., Afonso-Carrillo, J., Anadón, R., Araújo, R., Arenas, F., Arrontes, J., Borja, A., Díez, I., Duarte, L., Fernández, C., Tasende, M.G., Gorostiaga, J.M., Peteiro, C., Puente, A., Rico, J.M., Sangil, C., Sansón, M., Tuya, F., Bárbara, I., Juanes, J.A., Viejo, R.M., 2015a. Regresión de las algas marinas en la costa atlántica de la Península ibérica y en las Islas Canarias por efecto del cambio climático. ALGAS, Boletín Informativo de la Sociedad Española de Ficología 49, 5–12.
Martínez, B., Arenas, F., Trilla, A., Viejo, R.M., Carreño, F., 2015b. Combining physiological threshold knowledge to species distribution models is key to improving forecasts of the future niche for macroalgae. Global Change Biol. 21, 1422–1433.
McCoy, S.J., Kamenos, N.A., 2015. Coralline algae (Rhodophyta) in a changing world: integrating ecological, physiological, and geochemical responses to global change. Journal of Phycology 51, 6–24.
Méndez-Sandín, M., Fernández, C., 2016. Changes in the structure and dynamics of marine assemblages dominated by *Bifurcaria bifurcata* and *Cystoseira* species over three decades (1977–2007). Estuarine, Coastal and Shelf Science 175, 46–56.
Mercado, J.M., Niell, F.X., Gil-Rodríguez, M.C., 2001. Photosynthesis might Be limited by light, not inorganic carbon availability. In: Three Intertidal Gelidiales Species, vol. 149. The New Phytologist, pp. 431–439.
Micheli, F., Heiman, K.W., Kappel, C.V., Martone, R.G., Sethi, S.A., Osio, G.C., Fraschetti, S., Shelton, A.O., Tanner, J.M., 2016. Combined impacts of natural and human disturbances on rocky shore communities. Ocean & Coastal Management 126, 42–50.
Mineur, F., Arenas, F., Assis, J., Davies, A.J., Engelen, A.H., Fernandes, F., Malta, E.-j., Thibaut, T., Van Nguyen, T., Vaz-Pinto, F., Vranken, S., Serrão, E.A., De Clerck, O., 2015. European seaweeds under pressure: consequences for communities and ecosystem functioning. Journal of Sea Research 98, 91–108.
Niell, F.X., Soneira, A., 1976. Sobre la biología de *Ascophyllum nodosum* (L.) Le Jolis, en Galicia II. Biomasa total, estival, en la ría de Vigo. Investigación Pesquera 40, 105–110.
Nishihara, G.N., Terada, R., 2010. Species richness of marine macrophytes is correlated to a wave exposure gradient. Phycological Research 58, 280–292.
Piñeiro-Corbeira, C., Barreiro, R., Cremades, J., 2016. Decadal changes in the distribution of common intertidal seaweeds in Galicia (NW Iberia). Marine Environmental Research 113, 106–115.
Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., O/'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A., Richardson, A.J., 2013. Global imprint of climate change on marine life. Nature Climate Change 3, 919–925.
Porzio, L., Buia, M.C., Hall-Spencer, J.M., 2011. Effects of ocean acidification on macroalgal communities. Journal of Experimental Marine Biology and Ecology 400, 278–287.
Prathep, A., Lewmanomont, K., Buapet, P., 2009. Effects of wave exposure on population and reproductive phenology of an algal turf, *Gelidium pusillum* (Gelidales, Rhodophyta), Songkhla, Thailand. Aquatic Botany 90, 179–183.
Quintano, E., Díez, I., Muguerza, N., Figueroa, F.L., Gorostiaga, J.M., 2017. Bed structure (frond bleaching, density and biomass) of the red alga Gelidium corneum under different irradiance levels. J. Sea Res. 130, 180–188.
Santelices, B., 1991. Production ecology of Gelidium. Hydrobiologia 221, 31–44.
Short, J., Kendrick, G.A., Falter, J., McCulloch, M.T., 2014. Interactions between filamentous turf algae and coralline algae are modified under ocean acidification. Journal of Experimental Marine Biology and Ecology 456, 70–77.
Silva, J., Santos, R., Serôdio, J., Melo, R.A., 1998. Light response curves for *Gelidium sesquipedale* from different depths, determined by two methods: O_2 evolution and chlorophyll fluorescence. Journal of Applied Phycology 10, 295–301.
Southward, A.J., Hawkins, S.J., Burrows, M.T., 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. Journal of Thermal Biology 20, 127–155.
Stagnol, D., Michel, R., Davoult, D., 2015. Unravelling the impact of harvesting pressure on canopy-forming macroalgae. Marine and Freshwater Research 67, 153–161.
Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A., Tegner, M.J., 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation 29, 436–459.
Straub, S.C., Thomsen, M.S., Wernberg, T., 2016. Chapter 3: the dynamic biogeography of the anthropocene: the speed of recent range shifts in seaweeds. In: Hu, Z.-M., Fraser, C. (Eds.), Seaweed Phylogeography. Springer Science+Business Media, Dordrecht, pp. 63–93.
Takolander, A., Cabeza, M., Leskinen, E., 2017. Climate change can cause complex responses in Baltic Sea macroalgae: a systematic review. Journal of Sea Research 123, 16–29.
Torres, M., Niell, F.X., Algarra, P., 1991. Photosynthesis of *Gelidium sesquipedale*: effects of temperature and light on pigment concentration, C/N ratio and cell-wall polysaccharides. Hydrobiologia 221, 77–82.
Tueros, I., Borja, Á., Larreta, J., Rodríguez, J.G., Valencia, V., Millán, E., 2009. Integrating long-term water and sediment pollution data, in assessing chemical status within the European Water Framework Directive. Marine Pollution Bulletin 58, 1389–1400.
Tuya, F., Cacabelos, E., Duarte, P., Jacinto, D., Castro, J.J., Silva, T., Bertocci, I., Franco, J.N., Arenas, F., Coca, J., Wernberg, T., 2012. Patterns of landscape and assemblage structure along a latitudinal gradient in ocean climate. Marine Ecology Progress Series 466, 9–19.
Usabiaga, J.I., Sáenz Aguirre, J., Valencia, V., Borja, A., 2004. Climate and meteorology, variability and its influence on the ocean. In: Borja, A., Collins, M. (Eds.), Oceanography and Marine Environment of the Basque Country, vol. 70. Elsevier Oceanography Series, pp. 75–95.
Vilibic, I., Sepic, J., 2010. Long-term variability and trends of sea level storminess and extremes in European Seas. Global and Planetary Change 71, 1–12.
Voerman, S.E., Llera, E., Rico, J.M., 2013. Climate driven changes in subtidal kelp forest communities in NW Spain. Marine Environmental Research 90, 119–127.
Weisse, R., Bellafiore, D., Menéndez, M., Méndez, F., Nicholls, R.J., Umgiesser, G., Willems, P., 2014. Changing extreme sea levels along European coasts. Coastal Engineering 87, 4–14.
Wernberg, T., Connell, S.D., 2008. Physical disturbance and subtidal habitat structure on open rocky coasts: effects of wave exposure, extent and intensity. Journal of Sea Research 59, 237–248.
Wood, S.N., 2006. Generalized Additive Models: an Introduction with R. Chapman and Hall/CRC.